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ley of the Mackenzie, are found remains of *Sequoia*, *Taxodium*, *Thuya*, *Ulmus*, *Populus*, *Vitis*, *Platanus*, *Sapindus*, *Viburnum*, *Corylus*, *Juglans*, *Hicoria*, etc., etc. From this array we feel justified in assuming a cool to mild temperate climate for this early Eocene flora, and further, from the presence of numerous, often thick beds of lignite, that there was a much higher precipitation than at present.

A layer of fan-palm leaves a foot in thickness in a formation in northern Washington indicates climatic requirements in which the minimum temperature did not fall below 42° F. The presence of numerous West Indian types in the Miocene lake beds of Florissant, Colorado, would alone point to almost tropical conditions, but as these are associated with others of more northern affinities, it seems safe to predicate at least a warm temperate, or possibly sub-tropical climate.

II. THE RELATIONS OF PALEOBOTANY TO BOTANY

1. *Phylogeny and Taxonomy*

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It is impossible to disentangle morphology and phylogeny, for the largest motive in modern morphology is to construct phylogenies. An excessive amount of overlapping will be avoided in this paper by laying the emphasis upon the inferences to be drawn from morphological investigations as to probable lines of descent, rather than upon the morphological results themselves.

It should be kept clearly in mind that the material of paleobotany, as indicated by the program, is not always used to contribute to the science of botany. The determinations of plants in the interest of geological horizons are of immense service to geology, but of comparatively little value to botany. This means that some paleobotanists are geologists, and some are botanists, and it is the work of the latter that concerns us at this time.

The recent rapid development of our knowledge of the structures of fossil plants is familiar to botanists, constituting as it does one of the most remarkable chapters in the history of our science. This has been due not only to the elaboration of a technique for sectioning petrifications, but also to the inclusion of the vascular system among the morphological material that is recognized to be significant in conclusions concerning phylogeny. From the standpoint of paleobotany, the vascular system is its most valuable asset for vascular plants, for its chances of preservation exceed those of any other structures except the seed, and its significance in phylogeny is far more apparent and extended than that of the seed. As a result of this paleobotanical connection, the phylogeny of the vascular groups can be made now a resultant of comparative structures and actual history. Many an old phylogeny, based upon the comparative structures of existing plants alone, has been contradicted by history, which, in the nature of things, must furnish the final check upon any proposed phylogeny.

The topic of this paper is really an invitation to indicate some of the recent reactions of modern paleobotany upon the phylogenies of vascular plants. The title includes taxonomy, but in so far as this deals with great groups, defined or discovered, it is covered by the statements concerning phylogeny. So far as it deals with the recognition of individual forms, it is clear that paleobotany must learn to recognize the relationships of fossil plants, or there will be no reliable taxonomy or phylogeny. So long as paleobotany depended upon the form resemblances of detached organs, there could be no taxonomy in the real sense. It was merely a cataloguing of plant material. But when it learned to uncover structure, it began to establish a real taxonomy. The contributions of paleobotany to taxonomy, therefore, may be summed up in the statement that it has begun to extend our schemes of classification into the ancient floras; that this has resulted in a far truer view of the great groups

than their expression in the present flora can possibly give; and that this makes a rational phylogeny possible.

I will address myself in the main, therefore, to phylogeny, as involving all the taxonomy that is of large importance. When paleobotany to-day assembles the great series of paleozoic pteridophytes, the impression is very different from that of a few years ago. It is true that we have always heard of the giant forms of the Paleozoic and their dwarf representatives of to-day. We contrasted *Lepidodendron* with *Lycopodium*, and *Calamites* with *Equisetum*, and the total impression was the striking difference in size.

Now we have learned that these paleozoic Lycopodiales and Equisetales were not merely comparatively large, but that they were also comparatively complex. For example, we have learned that their huge bodies developed secondary wood and had attained heterospory. We begin to understand that vascular plants, with the exception of Angiosperms, were as completely differentiated, so far as the great groups are concerned, at the beginning of our records as now; and that the phylogeny in sight is not that of one great group following another, but of all the great groups spraying out into more and more modern expressions.

Not long ago, our morphology taught that the homosporous *Lycopodium* is the modern representative of the arborescent, paleozoic club mosses, and that the heterosporous *Selaginella* is a modern offshoot. Now we find that the paleozoic forms, with their heterospory, their ligules, and their other structures, link up with *Selaginella*; and we are asking, where are the ancestors of *Lycopodium*? Not long ago *Isoetes*, once suspected of being responsible for the monocotyledons, was fluttering between Filicales and Lycopodiales, and at last had settled down as an anomalous member of the latter group; and now modern paleobotany assures us that its whole structure suggests that it is a much reduced and compacted *Lepidodendron*. Thus the anomalous *Isoetes* has a ten-

tative connection, and the very normal *Lycopodium* has none.

Once we talked of the evolution of the strobilus as shown by *Lycopodium*, *Selaginella*, and *Equisetum*, and fancied that we saw in these modern forms the highest expression of the pteridophyte strobilus. Now we know that these strobili of to-day are excessively simple as compared with those of the Lycopodiales and Equisetales of the Paleozoic. The evolution of the pteridophyte strobilus that is in sight, therefore, is an evolution from a complex strobilus to a simple one.

According to the old morphology of external form, the club mosses were entirely capable of having given rise to the conifers. With some knowledge of structure this idea faded away, except in certain quarters, and the brilliant discovery of the so-called "seed-ferns" seemed to dispose of it entirely. Now we find among the paleozoic lycopods, notably some of the herbaceous ones, that a seed-like structure has been attained, and we have "seed-club mosses" as well as "seed-ferns." This does not mean that the club mosses gave rise to conifers or to any other existing group of seed plants, for more important structures forbid it; but it does mean that the paleozoic groups had advanced very far; that the seed-condition may have been attained by several groups of paleozoic pteridophytes; and that it takes more than a seed to distinguish a "seed-plant."

These are a few illustrations of the upsetting facts that modern paleobotany has been introducing into the old-time phylogenies of Lycopodiales and Equisetales.

It is among the phylogenies of Filicales, however, that modern paleobotany has wrought the greatest change, so far as pteridophytes are concerned. The old picture included a luxuriant fern vegetation during the Paleozoic, which culminated in the Coal-measures, whose so-called "fronds" made up at least one half the vascular flora. The occasional attached synangium or sorus was plainly like those of the Marattiaceæ, and since the *Marattias*

are eusporangiate, these paleozoic ferns were eusporangiate. And so we settled back comfortably to the conviction that the paleozoic ferns were Marattiaceæ, represented to-day by a small tropical family; that the eusporangiate habit and synangia are historically older conditions than the converse; and that the leptosporangiate habit and sori of free sporangia are comparatively modern.

The change of view that modern paleobotany has introduced must be familiar to most of you. The abundant fern vegetation of the Paleozoic has vanished, having been replaced by a great group of fern-like gymnosperms; many of the marattiaceous synangia have proved to be the microsporangiate structures of these same gymnosperms; there is no indication that the eusporangiate habit is older than the leptosporangiate; and it is entirely clear that our earliest known ferns had free sporangia and not synangia. In fact, after the first revolution of feeling, following the discovery of the fern-like gymnosperms, the question was seriously raised, is there any evidence of paleozoic ferns? Of course no one doubted their existence, but where is the evidence?

Paleobotany has now begun to answer this important question. Evidence of the existence of a group of arborescent, *Marattia*-like ferns during the Upper Carboniferous is accumulating. Much of this evidence is negative, for it consists simply of the fact that many species of certain of the large, so-called "frond genera" have not been found to be fern-like gymnosperms. On the doctrine of chance this may be worthy evidence. It simply means that a vast display of fern-like leaves must contain some ferns. The positive evidence, however, is supplied by vascular anatomy, and is found in the stems called *Psaronius*. The structure of these stems has been compared recently with the very characteristic structure of the stems of the living marattias, and the close relationship is obvious. Moreover, the leaves of *Psaronius* belong to one of the largest frond genera, and some of them bear

Marattia-like synangia. So clear is the evidence that Scott has called these arborescent *Marattias*, of the later Paleozoic, Palæo-Marattiaceae, and they may well stand for the precursors of the much humbler *Marattias* of to-day.

But these ancient *Marattia*-like forms were not the oldest ferns, for paleobotany has revealed a much older assemblage of undoubted ferns, so old, in fact, that the assemblage is called Primofilices. They are represented not only by numerous detached sporangia, many of which have the annulus characteristic of modern leptosporangiates, but all the essential structures of one well-characterized family, the Botryopterideæ, are known. These still somewhat vague Primofilices are extremely suggestive and perplexing. The free sporangia and the annulus of the Botryopterideæ suggest leptosporangiate connections; but the sporangia are not borne as among the leptosporangiates, nor is the annulus of the same character. The sporangia are in clusters terminating the bare branches of a rachis; and the annulus is a vertical, multi-seriate band on one side or both sides of the sporangium. In fact, the so-called "rudimentary" annulus of *Osmunda* suggests a reduced multiserial annulus of one of the Botryopterideæ. The vascular system, however, is very characteristic and very primitive, and is so varied as to suggest a synthetic type that might have given rise to all the diversities found in modern ferns.

The possibilities of paleobotany are well shown in connection with these Primofilices. One of its form-genera, *Stauropteris*, known only as sporangia, has been discovered by Scott with germinating spores. The germination of a fern spore is so different from that of a microspore of gymnosperms, or of any other heterosporous plant with which we are acquainted, that it is clear that *Stauropteris* is a fern sporangium and not the microsporangium of some gymnosperm. When germinating spores are preserved, and also the swimming sperms of paleozoic gymnosperms, as recently described, we may expect

that paleobotany will presently be able to uncover all of the essential morphology of the great fossil groups.

This picture of paleozoic ferns is somewhat dim yet, but were it not for the recent work in paleobotany we should have no picture at all, or, what is worse, an entirely false one.

The most conspicuous contribution of modern paleobotany, however, is its remarkably complete reconstruction of the phylogeny of gymnosperms. Our present records of this group extend through a longer period and are more continuous than for any other vascular group. It was not only associated with the paleozoic pteridophytes of the Coal-measures, but it was contemporaneous with pteridophytes throughout all their recorded history. Seed-plants, therefore, are just as old as any vascular plants, so far as our records go. It is clear that seed-plants have descended from pteridophytes, but when our records begin, they had already descended.

Our conception of gymnosperms before the paleobotanical work of the last decade, will emphasize the change that has taken place. We thought of them as cycads, conifers, and gnetums; and the morphology of that time undertook to develop a phylogenetic sequence with these three groups. Cycads were clearly the most primitive gymnosperms, and when *Ginkgo* was found to share with them in the retention of swimming sperms, it was just as clearly a "transition" form, on its way from cycads to conifers. In the dim paleozoic background Cordaitales lurked, but they were quite detached from living gymnosperms, a group that belonged to the geologist rather than to the botanist. I fancy that many a student of gymnosperms in those distant days never even heard of Cordaitales. The contrast between such a perspective of the group as I have just indicated and the perspective we possess to-day is due almost entirely to paleobotany.

In the first place, it resurrected the most primitive group of gymnosperms, the Cycadofilicales, called by our English brethren the Pteridosperms. It is a group that

had always been with us, disguised as paleozoic ferns, and the story of its recognition and rehabilitation is about the most sensational one in the annals of paleobotany. This meant that Cordaitales had a companion group, and that there were two great gymnosperm assemblages during the Paleozoic. Then the question arose as to the relationship of these two groups. There was no historical sequence to answer the question, for the two groups were observed side-by-side, and very distinct, as far back as the records go. This threw the answer back upon comparative structures, and this testimony is clear. If the two groups have been derived from ancient ferns, and the structure of Cycadofilicales hardly admits of any other conclusion, it is evident that the Cordaitales have departed much further from that origin. Therefore, if the two groups are related to one another genetically, and the discovery at various paleozoic horizons of persisting synthetic forms that combine features of both groups seems to make this reasonably assured, the Cordaitales were derived from Cycadofilicales older than any we know.

The beginning of our perspective, therefore, is that very ancient ferns, earlier than any of our records of vascular plants, gave rise to a Cycadofilicales stock, which persisted throughout the Paleozoic; and that this stock, also earlier than any of our records, gave rise to the Cordaitales branch. The records begin with these two stocks working along towards their modern expression, and all Mesozoic and modern gymnosperms can be referred to them. In other words, the gymnosperm genealogical tree comes into sight as two strong branches of a dichotomized trunk whose existence and character are hypothetical.

The Mesozoic branches from these two paleozoic stocks furnish us with another triumph of paleobotany, and this achievement is of peculiar interest to Americans.

The Cycadofilicales of the Paleozoic contributed to the Mesozoic the gymnosperms once known as "fossil cycads," a group so dominant and so characteristic that the

Mesozoic was long called "the age of cycads," so far as its vegetation is concerned. These characteristic Mesozoic forms are known now as the Bennettitales, and their resurrection from rich Mesozoic deposits of America is due to the skill and patience of our American colleague, Dr. Wieland. They retained many of the primitive features of the Cycadofilicales, but departed from them chiefly in the development of a strobilus. Not only so, but the strobilus is peculiar among gymnosperms, all of which have strobili except the fern-like Cycadofilicales. The strobilus of Bennettitales is bisporangiate, and the two sets of sporophylls are related to one another as they are in the flowers of Angiosperms. With the investment of sterile bracts, the strobilus as a whole bears a remarkable structural resemblance to such a flower as that of *Magnolia*. This resemblance has proved to be very seductive, for it has led to the claim that Bennettitales represent the ancestral forms of angiosperms. It is not the province of the present paper to discuss this claim. It has in it as a basis just enough of structural resemblance and of historical timeliness to make a plausible argument, but hardly enough to carry conviction to those who must take other facts into consideration. In any event, the Bennettitales are a notable group, and paleobotany has revealed them to us.

Along with them, the true cycads, or Cycadales, began to appear, apparently never a dominant group, and they have persisted in the tropics to the present time. The cycads as we know them, therefore, are the modern representatives of an old phylum, which included Bennettitales in the Mesozoic and Cycadofilicales in the Paleozoic, a phylum aptly called the Cycadophytes. The cycads present us with that paradox with which students of phylogeny are familiar, namely, they are structurally very primitive, but historically modern. So far from being the oldest of living gymnosperms, they are younger than the conifers and the ginkgos.

The Cordaitales of the Paleozoic had already developed

strobili, and had made notable changes in the vegetative body, changes which characterize the second great gymnosperm phylum, fittingly called the Coniferophytes.

The connections of the paleozoic Cordaitales with the Mesozoic ginkgos and conifers are very obvious, and these two groups, associated with Bennettitales and some Cycadales, made up the mesozoic gymnosperm flora. The Ginkgoales are really a mesozoic type, for their representation to-day by a single species is probably due to preservation by culture. It is an interesting fact that the ginkgos, directly connected with the paleozoic Cordaitales, have retained the primitive reproductive structures of that group and of the Cycadophytes, but advanced in vegetative structures as did the conifers. The group is very old in its reproductive methods, and modern in its vegetative body.

The great gymnosperm group of the Mesozoic, as of the present time, is the Coniferales, and their deployment during the Mesozoic is a subject of fascinating interest. The so-called tribes of conifers are found distinctly differentiated during the Mesozoic, and the determination of their relative ages is one of the triumphs of vascular anatomy. My colleague in this symposium, Professor Jeffrey, has lived in the storm center of this work, and it would not be fitting for me to invade his own special field. It may be said, however, that to discover that the Abietineæ (the pine tribe) are the oldest conifers is upsetting the older phylogeny fully as much as paleobotany has done for other gymnosperm groups.

The conifers are distinguished among the other gymnosperms that have been discussed, in being modern both in reproductive methods and vegetative structure. In contrast with cycads, therefore, they present the same paradox conversely, that is, they are structurally younger than cycads, but historically older.

This hasty outline of gymnosperm history, which paleobotany has interpreted for us, proves convincingly that no plant phylogeny is adequate until it has included

the historical record, which of course is the province of paleobotany; and furthermore, that general conclusions based upon the study of the living flora alone are more apt to be false than true.

The great problem of paleobotany to-day is the history of angiosperms. Having perfected a weapon in the attack upon gymnosperms, it remains for the paleobotanist who is a vascular anatomist to uncover the origin of our greatest group, with its comparatively brief history. The origin is probably recorded in the Mesozoic, and we wish to see the significant structures, and not guess at external form, and much less guess at purely hypothetical connections. To this great task paleobotany is turning. We have had the guesses; and I am confident that presently we shall have the facts.

II. THE RELATIONS OF PALEOBOTANY TO BOTANY

2. *Morphology*

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THE morphology of Goethe's metamorphoses, a hundred years ago, was entirely external morphology, illuminating at the time and for many decades later; but now for over a quarter of a century extinct, except so far as it lives on for descriptive purposes in manuals of systematic botany. It has been replaced by a conception of morphology, based not on external form but on internal structure. The replacement has been slow in this country, where, unfortunately, morphology is still very largely a thing of external threads and patches. The father of plant morphology in its modern form, was, as you all know, Wilhelm Hofmeister, who, over fifty years ago, began to put the subject on a truly evolutionary basis. Like many other men of genius, he was before his time and received little appreciation from his less progressive contemporaries.